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ON THE LIFE HISTORY OF AUTOLYTUS CORNUTUS AND ALTERNATE GENERATION IN ANNELIDS.

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THE claim for the presence of an alternation of generation in annelids owes its origin chiefly to the results obtained in study of the family of syllidians by the earlier authors, Milne-Edwards, Savigny, De Quatrefages, Krohn, and more recently by A. Agassiz. What subsequent proofs of the presence of this condition in annelids have been presented still find their strongest support in the phenomena observed in a division of this family, that of Autolytus.

In forms of Autolytus, like *Autolytus cornutus*, described by Agassiz, after the young and so-called asexual animal has attained a certain length, a new head is developed on the fourteenth setigerous segment, and in this way the individual becomes divided into what is known as the parent stock, including the original head with its segments, and the bud or stolon, including the new head with the remaining segments. The stolon contains the maturing sexual products, and after these reach a certain stage of maturity it separates from the parent stock and becomes free-swimming. The parent stock, as soon as the stolon is separated, regenerates the lost segments and in like manner develops a second and possibly a third or fourth bud. (In some forms of Autolytus (*A. varians*) the regeneration of new segments takes place before the shedding of the mature stolon, and thus a chain consisting of, at times, as many as eight stolons in different stages of development, becomes attached to the parent stock. In *Autolytus cornutus*, however, as in Proceræa, the stolon matures and becomes separated before an addition of new segments takes place, so that the parent stock of this form never bears more than a single stolon at a time.) During the process of separation the stolon undergoes such changes as are of service to it in the change of its life from among hydroids to that of surface swimming, the most conspicuous of which are the modification of the parapodia and the development of the swimming setæ. The sexual differences, as will be seen in comparing the free stolons, are also very conspicuous and appear quite early in the development of the stolon.

The free-swimming male stolon of an Autolytus was first described by Oersted, in 1843, as a new species of annelid to which he gave the name Polybostricus, while the free female stolon of another species (*Autolytus prolifera*) was similarly described by J. Müller, in 1853, under the name of Sacconereis. It was not until 1862, however, that Agassiz, in observing the separation of the stolon in *Autolytus cornutus*, demonstrated for certain the relation of the parent stock and stolons.

Alternate generation for annelids was first suggested by De Quatrefages in 1843, after observing a part of the budding process in a syllid (*Syllis monilaire*) previously described by Savigny ; later again by Krohn, in 1852, for *Syllis prolifera*, but the first complete description of the process was given by Agassiz, in 1862, in a paper entitled "On Alternate Generation of Annelids and the Embryology of Autolytus Cornutus." The development of the stolons of this syllid and their subsequent separation he followed stage by stage, and established the identity of the separately described Polybostricus and Sacconereis without a doubt. The stolons he described as sexual individuals which have been separated from the parent stock by a process similar to that of fission. The parent stock he regarded as distinctly asexual and as reproducing only by the separation and budding out of sexual stolons. A diagram of Agassiz's description of the cycle of generation would therefore be as follows :

Stolon = × < Eggs
Egg = Parent Stock
Stolon = × < Eggs

In this wise he attributed to *Autolytus cornutus* a distinct alternation of generation — in reality the only accurate alternate generation ever described for any annelid, and his original diagram of *Autolytus cornutus* still stands in some of our recent zoölogical text-books as a classical figure for the verification of alternation of generation in annelids.

The asexual condition of the parent stock is, however, not as constant as was supposed by Agassiz. In many of the specimens examined, particularly in individuals from which a first stolon has been separated, sexual products appear in the twelfth and thirteenth and even at times in the eleventh segment of the parent stock. At the time when the first stolon, *i.e.*, the stolon which originally formed a part of the body of the parent stock, becomes filled with sexual products none of the segments of the parent stock give any indication of the presence of reproductive products. In older individuals, however, in which apparently after a second or possibly a third stolon has been separated, I have found reproductive products in some stage of development in a large number of the specimens examined. Of such parent stocks found with reproductive products, by far the greater number were females, and of these I have been able to obtain individuals in which the ova had attained a size almost equal to that of mature ova. The different stages in the development of the sexual products I have been able to follow more successfully in a near relative of Autolytus, *Procerœa ornata*, the budding of which is in all respects similar to that of *Autolytus cornutus*. Of this species I have been able to find female specimens of parent stocks with ova in all stages of development up to the time when the ova are discharged from the body. The egg-sac, which it may be assumed also appears in these specimens, I have not been able to observe.

The external appearances of a parent stock with reproductive products in the stages of development in which I have been able to observe them differ very little from a parent stock in which no such products are as yet present. Occasionally I have found that the anterior eyes appear somewhat larger, but no modifications of the parapodia, such as would indicate the epitokal condition so common in other syllidians, were observed. In all sexually mature parent stocks of Proceræa I have found a third pair of eyes near the inner insertion of the palps. These are present as mere pigment spots in very young individuals of both Proceræa and *Autolytus cornutus*, but as a rule disappear or remain very inconspicuous in the adult. In several of the specimens in which the ova were nearest mature, conspicuous ventrally directed lenses were present. A similar development of this third pair of eyes I have observed in the epitokal syllid Odontosyllis, taken at a time when the eggs have reached complete maturity; so that the appearance of this pair of eyes in the parent stock of Autolytus at this time might, I think, be looked upon as partaking of the epitokal condition in other syllidians.

The percentage of parent stocks found with sexual products is by all odds too great to be looked upon as merely accidental. In a number of individuals examined, from all of which the stolons had recently been separated, and in which regeneration of segments was taking place (in this way eliminating as far as possible such individuals as are developing a first stolon), reproductive products were found to be present in as many as five out of twenty specimens examined for *Autolytus cornutus*, and in as many as six and sometimes seven out of twenty specimens of Proceræa examined. The stages of development of the reproductive products varied from early stages in which the presence of sexual cells could only be determined by the examination of sections to the more mature ova already referred to. By eliminating the apparently less mature individuals and selecting only such as would indicate by their size and general appearance that at least a second stolon had been separated, as many as ten to twelve out of twenty specimens were found to contain sexual products. Such conditions would strongly indicate that the presence of reproductive products toward the close of the phenomenon of budding is a constant stage in the life history of these syllids.

The life history of *Autolytus cornutus* would, therefore, consist in: (1) The development, from the egg, of the parent stock; (2) the development of sexual products in segments posterior to the thirteenth setigerous segment, the development of a head on the fourteenth, and the separation of these segments for the formation of the free-swimming stolons, Polybostricus (♂) and Sacconereis (♀); (3) regeneration of the lost segments and the formation in this way of a second and possibly a third or fourth stolon; (4) finally, the development in the parent stock of sexual products and the conversion of it into a sexual individual (Fig. 5). While the sexual products are forming, the regeneration of lost segments is still taking place, but in none of the specimens found had this new growth gone farther than the formation of a small bud, consisting of no more than eight or ten distinct segments.

As compared with a diagram of the cycle of generation as described by Agassiz, we would then have:

$$\begin{array}{rl} & \text{Stolon} = \times < \text{Eggs} \\ \text{Eggs} = & \text{Parent Stock} = \times < \text{Eggs} \\ & \text{Stolon} = \times < \text{Eggs} \end{array}$$

This would therefore be, not a sexual generation alternating with an asexual, but at most no more than a sexual dimorphism — a sexual individual budding off sexual stolons, and as its own sexual products mature, partaking more or less of the epitokal form of other syllids and itself becoming sexual.

Alternate generation has also been claimed for chain-forming syllidians, as Myrianide; but the presence of reproductive products in the posterior segments of the parent stock is of so common occurrence that the existence of such a generation has already prior to this been disputed by St. Joseph and Malaquin.

Korschelt and Heider in their text-book of *Comparative Embryology*, in accordance with the papers of Krohn and Agassiz, describe this process as a true alternation of generation, and hold it as distinctly different from the fission in Ctenodrillus, Protula, and Nais, in which all divided individuals are sexual and alike in all respects, and which, they assert, cannot be regarded as a true alternation of generation. They summarize the budding of Autolytus as "a process that is to be placed alongside that of strobilization in the Scyphomedusæ." The presence of reproductive products in the parent stock of Autolytus throws doubt upon this comparison, and it appears to me more plausible to place these forms alongside the processes described by Brooks for the Hydromedusæ (*Mem. Bost. Soc. Nat. Hist.*, Vol. III, No. 12). Particularly striking in this respect is the similarity in the life history of *Autolytus cornutus* to the life history of *Cunina octonaria*, which he gives in a diagram as follows:

Hydra = Medusa × < Eggs
Egg = Planula = Actinula = Medusa × < Eggs
Hydra = Medusa × < Eggs

Here, according to Brooks, there is asexual multiplication without alternation of generation. Since in *Autolytus cornutus* and Proceræa the parent stock also becomes sexual, just as does the actinula, we would have, in the life history of these syllids, nothing more than the parent stock undergoing asexual multiplication, and forming stolons just as in the asexual multiplication of the actinula to form hydra. Taking the meaning of alternation of generation, as defined by Brooks in his work on the Hydromedusæ, as the commonly accepted one, — a definition which is also in accord with the descriptions given by Korschelt and Heider, — we would have in the syllids, for which a true alternation of generation has been claimed, no alternate generation at all, but simply a dimorphism resulting from an asexual multiplication of the parent stock.

Without taking into consideration the morphological value of the stolon it would appear more plausible, therefore, to regard stolonization in Autolytus as a process akin to that of fission in other annelids — unlike the fission in Dero, Ælosoma, and other forms where the divided individuals are identical in all respects, in that it has direct reference to the distribution of the sexual products, yet similar to these in that all the resulting divisions are in reality sexual individuals.

Another aspect of this question is, however, presented by the morphological characters of the stolon itself. In the process of its development the stolon has been provided with a head very similar in structure to that of the parent stock, and with eyes even larger and more advantageously placed than those of the parent stock. The alimentary canal, moreover, is in a state of degeneration; the crowding of the reproductive products, particularly in the female stolon, has greatly reduced its calibre, and to all appearances it has ceased to function. Organs for the prehension of food are absent, a mouth-opening being formed simply by a union of the broken intestinal wall with the hypodermis, and it is quite evident, by the changes that have taken place in the alimentary canal of the mature stolon, and also by the continuous absence of food particles within it, that the stolon in its free-swimming stages does not feed. The stolon would then in reality reduce itself to a series of segments, some of which, in the male, or a large number of which, in the female, are gorged with reproductive products and provided with organs fitted for the proper distribution of the reproductive products — a condition similar to, but, by virtue of a head formation, more advanced than that which has been described for the sexual fragmentation in the Palolo worm. While the stolon must, for want of a better expression, be regarded as a distinct individual, in connection with the problem of alternation of generation the morphological value of such a structure might well be questioned.

The existence of a true alternation of generation in annelids so long as it is supported alone by the phenomena presented by Autolytus seems to me far from being established, and it is doubtful if a more extended study of any of the syllidians would add more to this proof. The presence of reproductive products in even a smaller percentage of parent stocks than were found in *Autolytus cornutus* or Proceræa could still hardly be looked upon as of purely accidental occurrence. Instead of regarding the presence of such sexual products in the parent stock of Autolytus as accidental, it seems to me more plausible to regard it as the continuance of a more primitive condition in which the animal *in toto* assumed, at the ripening of the sexual products, an epitokal form like that in Eusyllis, Odontosyllis, and Exogone, and stolonization as a secondary condition acquired for the purpose of a more perfect distribution of the sexual products. The complete epitokal changes in Autolytus have already been observed by Malaquin in *Autolytus lorgeferiens*, and described by him under the name of "epigamie," and it is very probable that a further study of the different species of Autolytus found along our coast would yield similar results. From our present knowledge it would appear that, as in *Autolytus cornutus*, the epitokal changes have been lost, or at least in greater or lesser part suppressed, in the parent stock of some syllids, and that in this way closely related forms of syllidians may exhibit sexual changes as various or more so than are shown in different species of Nereis; but it is very doubtful whether in any of our species the loss of sexual products has been so equally shared with these other changes as to leave a distinctly asexual parent stock.

The high development of the head of the stolon would form the strongest argument in favor of the distinct individuality of the stolon. Malaquin (*Recherches sur les Syllidiens*) has, however, already shown that the head of the stolon in different species of syllidians presents very different grades of development. In making this comparison he says: "L'individualisation du stolon diminue de plus en plus, au fur et à mesure qu'on suit la marche graduelle de ce phénomène. ——— autrement dit la tête qui marque pour ainsi dire le degré de perfectionnement de son individualité, se simplifie de plus en plus et arrive même à ne plus se former du tout." His figures, in which he compares the head of the stolon of *Haplosyllis hamata*, in the formation of which no development of a head takes place, with that of Trypanosyllis, in which a small head supplied with eyes is present, and, by different intermediate forms, with the complicated head structures of Autolytus, very clearly indicates, as had already been suggested by Huxley, that the stolon among syllids is not as distinctly individualized as would appear in observations on Autolytus by itself.

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